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Cacabelos, E

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Patchiness in habitat distribution can enhance biological diversity of coastal engineering structures

Eva Cacabelos[1,2]*, Richard C. Thompson[3], Afonso C. L. Prestes[2], José Manuel N. Azevedo[2], Ana I. Neto[2], Gustavo M. Martins[2]

[1]MARE – Marine and Environmental Sciences Centre, Caniçal, Madeira, Portugal

[2]cE3c - Centre for Ecology, Evolution and Environmental Changes/Azorean Biodiversity Group; Faculdade de Ciências e Tecnologia, Departamento de Biologia, Universidade dos Açores, Portugal

[3]Marine Biology and Ecology Research Centre, Plymouth University, UK

Correspondence:

E Cacabelos, MARE – Marine and Environmental Sciences Centre, Caniçal, Madeira, Portugal

Email: ecacabelos@mare-centre.pt

Abstract

1. Urbanization of coastal habitats is increasing worldwide. However, most man-made structures are poor surrogates for the habitats they replace and can strongly impact the diversity and functioning of coastal habitats.

2. The value of coastal engineering can be enhanced by the provision of microhabitats that facilitate colonization by marine life. One step forward is moved in this research by combining species coexistence theory, resource patchiness, and applied ecology in order to find ways that maximize the biological diversity of coastal defence structures.

3. Featureless areas of a seawall were modified by the addition of microhabitats (resource) that were distributed in different configurations of patchiness.

4. Gastropod diversity peaked at intermediate levels of microhabitat patchiness. This appeared to be driven by different patterns of resource use among species. Gastropods dispersed longer distances on unmodified seawalls than on natural rocky shores but when microhabitats were added dispersal decreased. The ability to find microhabitats differed among species.

5. Our results confirm that patchiness in microhabitat distribution affects biodiversity. The extent of microhabitat patchiness could potentially be tailored by coastal engineers to meet specific conservation priorities: increasing diversity vs. increasing number of individuals.

Keywords: benthos, coastal, ecosystem services, biodiversity, intertidal, invertebrates, urban development

1 INTRODUCTION

Coastal urbanization, the process whereby stretches of natural shoreline are modified or replaced by the addition of man-made coastal structures, is increasing worldwide (Firth, Knights, et al., 2016). Coastal urbanization is associated with a variety of negative impacts on the ecology of coastal habitats via changes in important physical, chemical and biological processes, which can strongly impact the structure and functioning of coastal habitats (Bishop et al., 2017; Heery et al., 2017; Nordstrom, 2014).

Generally, coastal defence structures are considered as poor surrogates for the natural shores they replace (Bulleri & Chapman, 2010; Chapman, 2003; Chapman & Bulleri, 2003; Coombes, La Marca, Naylor, & Thompson, 2015; Evans et al., 2015; Firth, Knights, et al., 2016; Moschella et al., 2005); when compared to natural habitats, coastal defence structures often support assemblages that are less diverse (Cacabelos et al., 2016a,b; Chapman, 2003, 2006; Chapman & Bulleri, 2003; Connell & Glasby, 1999; Evans et al., 2015; Firth et al., 2015; Firth, Mieszkowska, Thompson, & Hawkins, 2013; Moschella et al., 2005; Pister, 2009; Vaselli, Bulleri, & Benedetti-Cecchi, 2008). This effect has been attributed to the lack of topographic complexity that characterizes many of such structures (e.g. seawalls, pontoons, groynes) and which is important for many marine organisms (Aguilera, Broitman, & Thiel, 2014; Chapman, 2003; Metaxas & Scheibling, 1993; Moschella et al., 2005).

Recently, efforts to enhance the diversity on coastal defence structures showed that structures such as seawalls and breakwaters could be modified in an attempt to increase the biodiversity they support. This has included the addition of simple topographic features such as pits, grooves, cracks or water-retaining structures (Browne & Chapman, 2014; Chapman & Blockley, 2009; Coombes et al, 2015; Dafforn, Glasby, et al., 2015; Dafforn, Mayer-Pinto, Morris, & Waltham, 2015; Evans et al., 2015; Firth, Browne, Knights, Hawkins, & Nash, 2016; Firth, Mieszkowska, et al., 2013; Firth, Schofield, White, Skov, & Hawkins, 2014; Firth, Thompson, et al., 2013, 2014; Martins, Thompson, Neto, Hawkins, & Jenkins, 2010; Morris, Chapman, Firth, & Coleman, 2017; Morris et al., 2018; Strain et al., 2018 for a review). In order to further increase their ecological value, we need to understand how modifications made to coastal defence structures might affect species coexistence with potential long-lasting effects (Martins, Jenkins, Neto, Hawkins, & Thompson, 2016).

Much research, both theoretical and empirical, has focused on the mechanisms that determine diversity and local species coexistence such as resource partitioning (e.g. Schoener, 1974), predator-mediated effects (e.g. Leibold, 1996) and interference competition (e.g. Richards, Nisbet, Wilson, & Possingham, 2000; Vance, 1985). An important consideration is that spatial variability in the distribution of resources can promote coexistence by exploiting differences in foraging traits of competing species. This has been elegantly demonstrated by Chase, Wilson, and Richards (2001) who showed that coexistence (and hence species richness) in freshwater snails was driven by the interplay between differences in foraging trade-offs (ability to find a resource vs. ability to exploit

it) and patchiness in resource (patches of food) distribution. They found that diversity was greatest at intermediate levels of resource patchiness. These authors discussed findings in light of a digger-grazer model developed for marine snails (Schmitt, 1996; Wilson, Osenberg, Schmitt, & Nisbet, 1999) under which two competing species can coexist due to complementary foraging strategies: one species (coined as digger) excels at harvesting food in each patch, whereas the other species (coined as grazer) maximizes the area over which food is consumed. It was not possible for a species to simultaneously do both. Wilson et al (1999) also provided compelling evidence that the digger-grazer model may be much more widely applicable, including ecosystems such as the rocky intertidal.

In the north-eastern Atlantic, rocky shore snails (e.g. *Phorcus* spp., *Littorina* spp., *Patella* spp.) overlap considerably in spatial distribution and can all be found together on open rock. These grazer gastropods differ markedly in their feeding mode according to the morphology of their radula and feeding mechanism. For instance, docoglossan patellid limpets can penetrate hard substrates, taenioglossan littorinids can only penetrate softer substrates and rhipidoglossan trochids can only superficially brush the substrate surface (Hawkins et al., 1989). The way they use their radula to feed on algae has been likened to 'shovels', 'rakes' and 'brooms', respectively (Steneck & Watling, 1982). Moreover, these species differ remarkably in the way they move. Patellid limpets are known for their homing behaviour, the consistent return of individuals to a specific location on the substratum when not feeding or searching for food (Lord, 2008; Santina, 1993; Shanks, 2002; Steneck, 1982). In contrast, trochids and littorinids show

133 little site fidelity and gradually disperse away to locate new patches with
134 resources (Chapman, 1995; Norton, Hawkins, Manley, Williams, & Watson,
135 1990). They must either move faster between patches or convert more
136 efficiently the resources to population growth (Richards et al., 2000) than
137 species exhibiting homing behaviour.
138
139 For many intertidal snails, however, food is not the only important resource
140 (Rochette & Dill, 2000). Intertidal microhabitats such as rockpools, pits and
141 grooves also play an important role, at least during some stage of their life-cycle
142 (Firth & Crowe, 2010), by dampening environmental extremes during low water
143 (Fairweather, 1988; Gray & Hodgson, 1998) and/or providing protection from
144 predation (Bertness, Garrity, & Levings, 1981; Garrity, 1984). In fact, most
145 enhancements done to coastal defence structures (see above) are effective
146 because they provide a refuge for environmental stressors or the risk of
147 predation (Browne & Chapman, 2011, 2014; Chapman & Blockley, 2009;
148 Coombes et al., 2015; Evans et al., 2015, 2017; Firth, Browne, et al., 2016; Firth,
149 Knights, et al., 2016; Firth, Mieszkowska, et al., 2013; Firth, Schofield, et al., 2014;
150 Firth, Thompson, et al., 2013, 2014; Loke, Ladle, Bouma, & Todd, 2015; Martins
151 et al., 2010, 2016; reviews in Dafforn, Glasby, et al., 2015; Dafforn, Mayer-Pinto,
152 et al., 2015; Firth, Knights, et al., 2016; Strain et al., 2018). However, the
153 magnitude of the effects varied among considered functional groups and habitat
154 settings (Strain et al., 2018). For instance, Martins et al. (2016) showed that the
155 response of three intertidal snails to the addition of pits to a topographically
156 simple seawall varied according to pit size and number: littorinids (*Tectarius*
157 *striatus* and *Melarhaphe neritoides*) tended to aggregate on small microhabitats,

158 limpets (*Patella candei*) tended to aggregate in areas with large microhabitats,
159 whilst all species tended to be more abundant with increasing microhabitat
160 density. Moreover, the contrasting response of limpets and littorinids to
161 microhabitat size had community-wide cascading effects, leading, in the longer-
162 term, to the establishment of very distinct assemblages. Martins et al. (2016) also
163 noted that whilst many individual littorinids were often found aggregating in a
164 single pit, limpets were generally found alone (one individual limpet per pit).
165 This pattern suggests that inter- and intra-specific competition (for pits) is
166 higher for limpets than among littorinids.
167
168 In the present study we build on previous findings (Martins et al., 2010, 2016) to
169 test if spatial variability (patchiness) in the distribution of microhabitats (pits)
170 can affect snail behaviour and be used as a means to enhance diversity in coastal
171 defence structures.
172 We hypothesize that (1) intertidal gastropods have distinct displacement
173 behaviours on seawalls and natural rocky shores, (2) patterns of gastropod
174 dispersal and microhabitat use differs among species; specifically, littorinids (*M.*
175 *neritoides* and *T. striatus*) disperse further and utilise experimental pits more
176 quickly than limpets, and finally (3) richness in gastropod snails will be
177 enhanced at intermediate levels of microhabitat patchiness, reflecting the
178 divergent patterns of motility, intra- and inter-specific competition among these
179 species.
180
181 **2 METHODS**
182 **2.1 Study sites and gastropod assemblages**

183 The Azores archipelago is volcanic by origin and the coast is mainly composed of
184 boulder shores interspersed between rocky platforms. The tides are semidiurnal
185 and the tidal range small (< 2 m). The experimental study was done on a natural
186 rocky shore platform and the adjacent steep seawall consisting of large regular-
187 sized basalt blocks, comprising a stretch of the coast of 200 m with south-
188 southwest orientation at São Roque (São Miguel Island). The basalt blocks had a
189 smooth surface and lacked the microtopographic complexity of the surrounding
190 natural rocky shore (see Martins et al., 2010). The assemblage of grazer
191 gastropods from mid to upper shore levels comprised the limpet *Patella candei*
192 and the littorinids *Tectarius striatus* and *Melarhaphe neritoides* (Martins,
193 Thompson, Hawkins, Neto, & Jenkins, 2008), both in natural shores and seawall.
194 These are, for the most part, the only macroinvertebrate grazing gastropods
195 present in the intertidal throughout the archipelago. Other species (e.g. *Littorina*
196 *saxatilis*) are rare on Azorean coasts.
197
198 **2.2 Dispersion behaviour on seawalls vs. natural rocky shores**
199 Since patterns of dispersion on seawalls have been shown to differ from those
200 observed on natural rocky shores (Bulleri, Chapman, & Underwood, 2004), it
201 was important to test, prior to the main experiment, if the same occurred in the
202 study system and focal species. To compare the movement of gastropods in each
203 habitat (seawall and natural rocky shore), the distance travelled per unit time on
204 both habitats was investigated during the summer of 2014. On the seawall and
205 on an adjacent natural rocky shore (a platform shore with the same orientation
206 100 m apart), random sites metres apart were selected at similar intertidal level
207 and animals were individually labelled. We calculated the distance travelled over

208 different periods of time (1 and 14 days) by measuring the distance between the
209 animals and two fixed marks. The distance travelled over the different periods of
210 time was calculated by co-ordinate geometry, using paired measures at the
211 beginning and at the end of the period of time (Underwood 1977). As many
212 individuals were lost, we repeated the procedure described several times to
213 obtain enough replicates. For the purpose of analyses (see below), data from
214 each time period were pooled together.
215
216 The distances travelled by gastropods on the seawalls and the natural rocky
217 shore were compared using a two-way permutational ANOVA (PERMANOVA,
218 Anderson, 2005) with the factors 'Habitat' and 'Species' fixed and orthogonal to
219 each other. The analyses were done separately for 1 and 14 days after the start
220 of the experiment. Permutational ANOVA was used instead of traditional ANOVA
221 because analyses were unbalanced (e.g. different numbers of animals per
222 species). Prior to analyses, heterogeneity of variances was checked using
223 PERMDISP and transformations were applied where necessary. Pair-wise
224 comparisons were made when differences were found. All analyses were run on
225 Euclidean distances with 999 permutations using the software PRIMER 6+
226 (Clarke & Gorley, 2006).
227
228 **2.3 Microhabitat patchiness**
229 In December 2013, two sites 50 m long, belonging to the same continuous
230 seawall, located 100 m apart and similarly exposed to oceanic swell, were
231 selected for experimental manipulation. To test the effect of patchiness on
232 gastropod diversity, 20 plots (25 x 25cm) were haphazard marked at mid-shore

233 level (approximately 1.50-1.90 m above lowest astronomical tide) of each site,
234 where barnacles, limpets and littorinids are present, and randomly assigned to
235 four treatments (n = 5): control (no pits added), low, intermediate and high
236 levels of microhabitat patchiness (Figure 1). Comparison of controls and
237 treatments were used to confirm that all the three species, *M. neritoides, T.*
238 *striatus* and *P. candei*, responded positively to the experimental addition of pits,
239 (see Martins et al., 2016). To ensure that the sizes of experimental pits were
240 suitable for the majority of the individuals, the total number and size of pits was
241 established *a priori* according to previous observational and experimental
242 studies in the area (Martins et al., 2010, 2016). As pits can be key features for the
243 recruitment and survival of many species, especially for the case of juvenile
244 stages (e.g. recent recruited and immature limpets < 1cm), and the effect of pit
245 density and size for small limpets was limited by the density of pits, whatever
246 their size (Martins et al., 2010), here we opted for drilling pits 12 mm diameter,
247 10 mm depth. Levels of patchiness were achieved by drilling 16 pits within the
248 plot areas at varying arrangements following the design of Chase et al. (2001): a
249 unique group of 16 adjacent pits (low patchiness), two groups of 8 adjacent pits
250 in opposite corners of the plot (intermediate patchiness) and four groups of 4
251 adjacent pits, each on a different corner of the plot (high patchiness) (Figure 1).
252
253 Martins et al. (2016) found that patterns of pit use on rocky shores differed
254 slightly between the short (3 months to 1 year) and the long-term (7 years),
255 probably reflecting the adjustment of animal densities to intra- and inter-specific
256 competition. To allow plenty of time for individuals to relocate, experimental

plots were only sampled in June 2016, 30 months after experimental setup, when all gastropods within experimental plots were identified and counted.

The effects of microhabitat patchiness on the diversity (species richness and Shannon index of diversity) and abundance of gastropods was investigated using a two-way mixed model ANOVA with the following factors: 'Site' (random with two levels) and 'Treatment' (fixed with 3 levels: low, intermediate and high), orthogonal between them. Prior to analyses, data were inspected for heterogeneity of variances using Cochran's test, and transformations were applied where necessary. *Post-hoc* pooling was done at $p>0.25$, by pooling MS terms and using the resultant term as the denominator for the *F*. *A posteriori* comparisons were made using the SNK test when differences were found. Pearson correlation coefficient was calculated among all gastropod species across treatments to evaluate potential biotic interactions among these species.

2.4 Dispersion behaviour across microhabitat patchiness

We compared the dispersal of gastropods across levels of patchiness in the winter of 2016-2017 at one of the experimental sites. Prior to the start of the experiment, plots were defaunated. Afterwards, *M. neritoides, T. striatus* and *P. candei* were collected from the surrounding area within the seawall, marked with coloured nail varnish and translocated to the centre of each experimental plot (5 individuals per species per plot). In the case of *P. candei*, more sensitive to manipulation, the use of smaller animals allowed us to easily dislodge them off the rock. Moreover, animals were carefully removed and immediately translocated to the experimental plots. Adherence of animals was checked about 30 minutes

282 afterwards. In most cases limpets reattached alone, but if not these were replaced.
283 The number of animals transplanted into each plot was within the range of
284 densities observed on several natural shores of the island (mean values of
285 12.8±5.0, 11.7±3.4 and 4.1±0.6 individuals per 625 cm^2 were observed for *M.*
286 *neritoides*, *T. striatus* and *P. candei* respectively, during summer 2013 (n=25,
287 Cacabelos et al., 2016a). In January 2014 we observed even higher densities on
288 local natural shores (103.6±13.0 *M. neritoides* individuals per 625 cm^2, 24.8±5.4
289 *T. striatus* and 5.3±0.9 *P. candei* (n=30) and therefore intra-species competition
290 was not expected to occur. After 24h, we measured the distance travelled by each
291 marked individual from the centre of each plot and recorded whether it was inside
292 or outside a pit. To account for the number of animals which were lost, we
293 repeated the procedure described two more times (total of 3 runs for *P. candei* and
294 2 for littorinids).
295
296 To test the hypothesis that dispersal of gastropod species differed among levels
297 of patchiness, for each individual we calculated its dispersal from the centre of
298 the patch against the mean dispersal observed on controls (no pits) using the Ln
299 ($d_{treatment}/d_{control}$), d = distance travelled from the centre of the plot. This was
300 done to standardize the distances travelled among species and against a
301 situation where no microhabitats were available (controls). Negative values
302 indicate that animals dispersed less than in controls, while positive values
303 indicate that animals dispersed more than in controls. Data were analysed using
304 a 2-way factorial permutational ANOVA with the following factors: 'Species' (3
305 levels) and 'Treatment' (3 levels: low, intermediate and high), both fixed. Pair-
306 wise comparisons were made when differences were found. Again,

permutational ANOVA was chosen due to the unbalanced dataset (for further details see above). For analysis, data from the different runs were pooled together.

3 RESULTS

3.1 Dispersion behaviour on seawall vs. natural rocky shore

In the shorter-term (1 day), distances travelled by *Tectarius striatus* were always significantly greater than those travelled by *Melarhaphe neritoides* and *Patella candei* (mean ± SE, *T. striatus*: 12.0 ± 2.2 cm, *M. neritoides*: 3.9 ± 0.9 and *P. candei*: 1.8 ± 0.5 cm), but there were no differences in dispersal between habitats (natural rocky shore or seawall (Figure 2, Table S1). However, in the longer-term (14 days) there was a significant interaction between habitat and species (Table S1). Pair-wise comparisons showed that, on average, limpets dispersed very little regardless of habitat but that littorinids dispersed significantly greater distances on the seawall than on the natural rocky shore (Figure 2, Table S1). Pair-wise comparisons also showed that while on natural shores *M. neritoides* dispersed little (similar to *P. candei*), on the seawall *M. neritoides* dispersed much more (similar to *T. striatus*) (Table S1).

3.2 Suitability of experimental microhabitat addition

The addition of experimental pits to the seawall proved a successful means to enhance the diversity and abundance of gastropods per unit area (Table 1): compared to controls, experimentally enhanced plots supported, on average, an abundance of individuals and a species richness that was 1 order of magnitude greater.

3.3 Microhabitat patchiness

When considering the effects of the different spatial arrangements of experimental pits, both the species richness and the Shannon diversity generally peaked at intermediate levels of patchiness (Figure 3). In fact, mean species richness at intermediate patchiness was significantly greater that found on high patchiness (Figure 3; see also Table S2 in supporting information for ANOVA tables). Shannon diversity was also significantly greater at intermediate patchiness compared to low and high patchiness (Figure 3, Table S2). For both richness and Shannon diversity, results were spatially consistent in both sites examined (Table S2).

Statistical analyses failed to detect any significant variation in mean abundance of the different species among levels of patchiness, probably because there was much (and significant) spatial variability between sites for both *P. candei* and *M. neritoides* (see Table S3). However, when the numbers of all individuals per treatment were pooled together, the pattern varied substantially and we observed differences among species (Figure 4): the numbers of *T. striatus* increased with patchiness, whereas the numbers of both *P. candei* and *M. neritoides* peaked at intermediate levels of patchiness.

A negative correlation was found between the numbers of limpets and both species of littorinids (*P. candei* * *T. striatus*, r = -0.34; *P. candei* * *M. neritoides*, r = -0.18), whereas a positive correlation was found between the numbers of littorinids (*T. striatus* * *M. neritoides*, r = +0.44).

3.4 Dispersion behaviour across microhabitat patchiness

All species tended to disperse less in areas enhanced with experimental pits (Figure 5a). There were also significant differences in dispersal both among species and among treatments. Inspection of a posteriori comparisons showed that *P. candei* and *M. neritoides* dispersed significantly less than *T. striatus* (Table S4). Patterns of dispersion also varied across levels of patchiness, with all animals dispersing significantly less in areas with low patchiness (Figure 5a). Inspection of the experimental plots after 24h showed that the proportion of individuals (data pooled over replicates) found inside pits decreased with increasing patchiness (Figure 5b).

DISCUSSION

The main outcome of this study was that diversity, both in terms of richness and Shannon diversity, was greater at intermediate levels of microhabitat patchiness. This is in accordance with Chase et al. (2001) who found that the diversity of freshwater snails was also greatest at intermediate levels of resource patchiness. In their study, this pattern was driven by the interplay between differences in foraging trade-offs, coexisting due to complementary foraging strategies (Schmitt, 1996; Wilson et al., 1999), and patchiness in resource distribution, and thus highlight the importance of variability in species traits. Previous studies in natural systems demonstrated how the responses of species assemblages to microhabitats can vary among taxa (Bateman and Bishop, 2017). Here, too, we showed that not only the dispersal of intertidal gastropods varied among species, especially between littorinids and limpets which have contrasting

382 foraging behaviours (different abilities to find and exploit resources), but also
383 between habitats (natural rocky platform and seawall) and between levels of
384 habitat patchiness on a seawall.
385
386 A mechanism to explain the biotic response to microhabitat manipulation can be
387 deduced from the observation that littorinids (but not limpets) dispersed over
388 larger distances in seawalls compared with natural rocky habitats, a result also
389 shown for the limpet *Cellana tramoserica* on seawalls in New South Wales
390 (Bulleri et al., 2004). This greater mobility on artificial substrates suggests that
391 gastropods move more because they may lack appropriate microhabitats (e.g.
392 pits) in which to shelter. This hypothesis is further supported in our study by the
393 result that all species also dispersed less in areas of the seawall enhanced with
394 pits. In addition, complementary information, e.g. related to the age of the
395 animals, could be incorporated when predicting patterns of movement of
396 gastropods (Crowe, 1996). The three species also exhibited distinct short-term
397 patterns of dispersal in relation microhabitat patchiness. Although not
398 experimentally tested, we found evidence that at least limpets and littorinids
399 may be competing for these microhabitats on the seawall. As such, the
400 differential ability to disperse may be important in alleviating competition
401 among these species, which could, in the longer term, result in the distinct
402 patterns of abundance observed among treatments and hence, diversity. Our
403 results thus suggest that the manipulation of microhabitat patchiness may be an
404 effective way to exploit differences in species dispersal, and presumably foraging
405 behaviour, and which may in fact have wider implications for the structure of
406 remainder of the community (Martins et al., 2014; O'Connor & Crowe, 2005).

Understanding the mechanisms that drive species coexistence has been a central question in theoretical ecology, but it may have wider applied interest. The addition of microhabitats to an existing seawall without previously water retaining features was shown to be an effective way to enhance the local numbers and diversity of gastropods, confirming previous studies (Martins et al., 2010, 2016) and suggesting the potential use of such modifications as a means to enhance the diversity of intertidal biota on coastal defence structures (see Firth, Knights, et al., 2016 and references therein). Here we show that controlling the spatial patchiness of microhabitats is an effective way to enhance the local abundance or diversity of target species in artificial substrates. However, a frequent limitation of eco-engineering research is the investigation of large-scale effects or habitat modifications (but see Morris et al., 2017). Although our experiments have been replicated at sites within a single artificial structure, a next step would be to evaluate the effect size of such treatments at the scale of the entire structure, on different geographical areas and with different assemblages of organisms. Provided that results hold, this study suggests that managements strategies could potentially be tailored to meet specific conservation priorities and inform eco-engineering approaches to enhance biodiversity, namely increasing diversity vs. increasing number of individuals.

This work emphasizes the importance of field experiments as a powerful tool to establish causal relationships and adds to the toolkit of coastal engineers in the design of more ecologically friendly coastal structures, providing direct evidence of the suitability of low-cost engineering modifications to enhance artificial

ecosystems. Our study adds to the wider literature showing that coastal structures can be enhanced in different ways: (i) via the provision of different microhabitat types (e.g. pits, grooves, rockpools) (e.g. Browne & Chapman, 2014; Coombes et al., 2015; Firth, Schofield, et al., 2014; Firth, Thompson, et al., 2014), (ii) via the provision of microhabitat of different sizes (Martins et al., 2010, 2016), or (iii) by controlling the level of patchiness in the provision of microhabitats (this study). Ultimately, the choice among these options should be dictated by the desired outcome (e.g. ecological, conservation of exploited species) and by the available intervention possibilities.

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668 **TABLES**

669 **Table 1**. Mean (± SE) numbers and richness of gastropods found on plots with

670 experimental pits added (n = 30) and unmanipulated controls (n = 10).

	P. candei	*T. striatus*	*M. neritoides*	Richness
Treatment	2.27 ± 0.89	22.37 ± 4.44	2.43 ± 0.93	1.73 ± 0.17
Control	0.10 ± 0.10	0.40 ± 0.22	0.20 ± 0.13	0.60 ± 0.27

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690 **FIGURE CAPTIONS**

691 **Figure 1**. Different levels of patchiness obtained by drilling 16 pits (12 mm
692 diameter, 10 mm depth) within the plot areas, achieving (a) low, (b)
693 intermediate and (c) high patchiness. In Control plots (d), no pits are added.

694 **Figure 2**. Mean (+SE) dispersal of tagged individuals of *P. candei, T. striatus* and
695 *M. neritoides* on seawalls and natural rocky shores after (a) 1 and (b) 14 days.
696 Letters highlight significant differences among means as detected by *a posteriori*
697 comparisons (see Table S1 for further details).

698 **Figure 3**. Mean (+SE) grazing gastropod (a) richness and (b) Shannon diversity
699 in experimental enhanced areas of the seawall after 30 months at increasing
700 levels of the patchiness in the spatial distribution of pits. Letters highlight
701 significant differences among means as detected by *a posteriori* SNK tests (for
702 further details see Table S2)

703 **Figure 4**. Total number of individuals of (a) *P. candei*, (b) *T. striatus* and (c) *M.*
704 *neritoides* found after 30 months in experimentally enhanced areas of the
705 seawall at increasing levels of microhabitat patchiness.

706 **Figure 5**. (a) Mean (±SE) dispersal relative to controls among gastropod species
707 across all levels of microhabitat patchiness after 24h. Letters highlight significant
708 differences among means as detected by pair wise comparisons (for further
709 details see Table S4); (b) Proportion of relocated gastropods found inside pits
710 after 24h.